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Effects of Changing Levels of UV Radiation on Plant and Timber Production

Presented by
The Food and Agriculture Organization

Effects of Changing Levels of UV Radiation on Plant and Timber Production [1]

Introduction

The ozone layer is the principal shield preventing harmful short-wave ultraviolet radiation from reaching the surface of the earth. Suggestions that man's activities may be leading to a moderate reduction of the stratospheric ozone layer is of justifiable concern. Several threats such as exhaust emissions from high altitude aircraft and halomethanes diffusing up from the troposphere appear to have a sound theoretical support to serve as a basis of concern. Several other threats such as a contribution of NO_2 to the stratosphere from the widespread use of nitrogen fertilizers are more questionable though of sufficient magnitude to warrant further investigation. The several potential causes of stratospheric ozone reduction would have more or less additive effects. Ozone reduction would take place over long periods of time and would not be quickly reversible.

The threat to higher plants used in agriculture and timber production is of particular concern since plants have evolved to be efficient collectors of solar radiation which is of necessity in effective photo-synthetic energy capture. This also maximizes exposure of plant leaves and shoots to solar UV radiation. Any threat to plant productivity, no matter how subtle, is of concern in view of the existing global demands for food and fiber production.

Unfortunately, it is presently impossible to predict the magnitude of the effect on plant life due to any particular stratospheric ozone reduction. Most of the effects on plants are of a detrimental nature. However, the increased UV radiation that would occur with moderate reduction in stratospheric ozone concentrations would probably result in rather subtle effects on plants. Therefore, it is very difficult to quantitatively assess the overall magnitude of the potential threat - particularly when contemplating global crop production or the productivity from forests. Even though many effects would be subtle, this does not lessen the cause for concern, particularly when a perturbation of global proportions and long time constants is being considered. This paper will present a problem statement as to the nature of the effects presently anticipated and attempt to bring this threat into context relative to the natural fluctuations to ozone that are already known to occur.

Basic Biological Implications of Ozone Reduction

The waveband of concern in the ozone reduction question is confined to a rather small part of the solar UV spectrum. Of particular potential detriment to biological systems are wavelengths shorter than 315 mm since nucleic acids and proteins have an appreciable absorption cross section in this waveband. The absorption cross section of ozone also becomes appreciable only at wavelengths shorter than 315 mm. With decreasing wavelengths, the ozone absorption coefficient increases exponentially (Fig. 1). Even though the average total atmospheric ozone column is only on the order of 3 mm if condensed to standard

[1] Paper compiled from the work of Prof. M.M. Caldwell and Dr. E. Wellmann

temperature and pressure (commonly denoted as 0.300 atm.cm), it is sufficient to effectively attenuate the solar UV flux to less than $10^{-3} W \cdot m^{-2} \cdot nm^{-1}$ at wavelengths below 295 nm. If the atmospheric ozone column were reduced to only 10% of this thickness, calculations using the model of Green et al., (27) suggest that UV irradiance at ground level, with the sun directly overhead, would still not include wavelengths shorter than 280 nm at intensities greater than $10^{-3} W \cdot m^{-2} \cdot nm^{-1}$. Thus, any consideration of biological effects of increased solar UV flux resulting from reduced atmospheric ozone must be confined to the waveband between 280 and 315 nm (commonly designated as UV-B) and for moderate ozone reduction only the 290 to 315-nm waveband would be of concern.

With changes in optical thickness of the atmospheric ozone column there is a predictable change in ground-level UV-B irradiance as illustrated in Fig. 2. As would be expected from the ozone absorption coefficient, a change in ozone thickness is reflected much more in spectral irradiance at shorter wavelengths. The greater representation of shorter wavelengths with reduced ozone should be of biological importance if the biological effectiveness of UV-B radiation corresponds to the action spectra for effects as mediated by nucleic acid and protein chromophores as shown in Fig. 1. To accommodate this relationship, a useful expression of biologically effective UV-B irradiance, $UV\text{-}B_{BE}$, can be defined as

$$UV\text{-}B_{BE} = \int_{280}^{315} I_\lambda \cdot E_\lambda \cdot d\lambda \qquad (1)$$

where I_λ is the spectral irradiance at wavelength λ, and E_λ is the relative biological effectiveness at wavelength λ as defined by Caldwell (11). This effectiveness term closely approximates the action spectra for biological effects involving nucleic acid and proteins as shown in Fig. 1 in the 280 to 315-nm waveband. This function was, however, derived from a range of action spectra for both higher and lower plants involving several physiological responses as shown in Fig. 3. Except in the case of 3I, the chromophores were considered to be nucleic acid or protein compounds. Despite the fact that action spectra can be modified by wavelength-dependent filtration through plant tissues covering physiological targets, the correspondence of this sundry of action spectra is reasonably good. In the case of 3I, which deviates most from the generalized spectrum, the chromophore was considered to be a plant hormone, indoleacetic acid. Although the number of available action spectra for physiological phenomena of higher plants in the UV-B is quite limited, some generality of this E_λ relationship still seems reasonable. When the effects of decreasing atmospheric ozone concentrations on UV spectral irradiance is calculated (27) and integrated with respect to biological effectiveness according to equation 1, the net effect is an approximate 2% increase in $UV\text{-}B_{BE}$ for each 1% decrease of the atmospheric ozone column.

Although UV photobiology has progressed far during the last few decades, this research has only occasionally involved higher plants and has been primarily concerned with the effects of 254-nm radiation. Nearly monochromatic radiation of this wavelength can be easily generated by low-pressure mercury lamps and this conveniently falls within the waveband of maximum inactivation cross section of nucleic acids. Although much of what has been learned (particularly the elucidation of various radiation repair mechanisms) may also likely apply to the response of higher plants to UV-B radiation, a simple extrapolation or prediction of ecological consequences of ozone depletion cannot be made from this information.

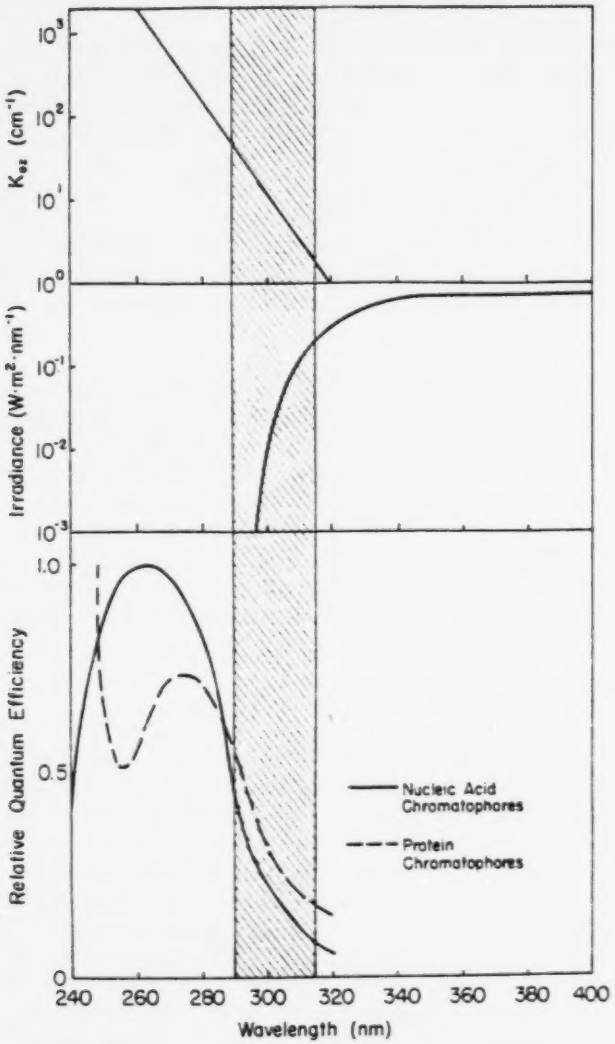

Figure 1. Ozone extinction coefficient adapted from Green et al., (27); the solar ultraviolet flux (direct sun plus diffuse sky radiation) at ground level for conditions of 0.300 atm.cm ozone thickness and a solar angle of 30° from the zenith taken from calculations using the model of Green et al. (27) and measurements of Bener (6); generalized action spectra for biological responses to UV radiation involving protein (dashed line) and nucleic acid (solid line) chromophores. Adapted from Giese (25). The hatched area designates that portion of the spectrum which is involved in the stratospheric ozone depletion question.

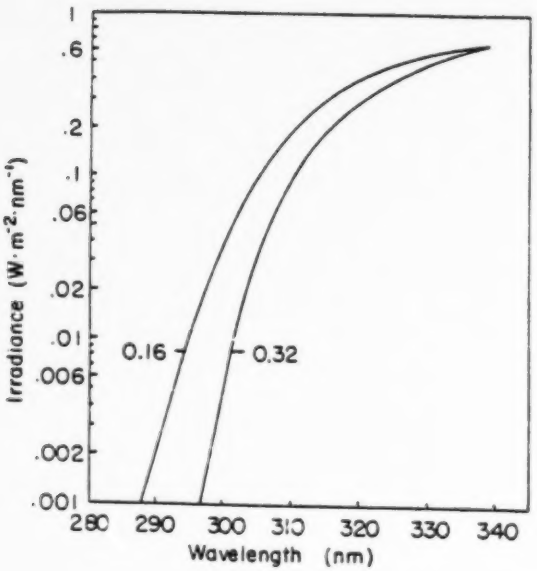

Figure 2. Global (direct sun plus sky) spectral irradiance calculated for a solar angle of 30° from the zenith and atmospheric ozone concentrations of 0.32 and 0.16 atm.cm from the model of Green et al.

Not only are there appreciable differences in the quantitative responses to UV-B radiation as opposed to 254-nm radiation as is indicated by the action spectra for physiological responses, but there may also be qualitative differences in the patterns of response as has been demonstrated by Bachtwey (44) for phytoplankton. Furthermore, most higher plants have apparently evolved defense mechanisms to minimize the UV-B radiation insult. These include absorption of UV-B radiation in outer tissue layers and molecular repair mechanisms such as photoreactivation and dark repair systems. Thus, of ultimate biological interest is the net unrepaired UV-B-induced damage that would result in nature if the ozone layer were diminished.

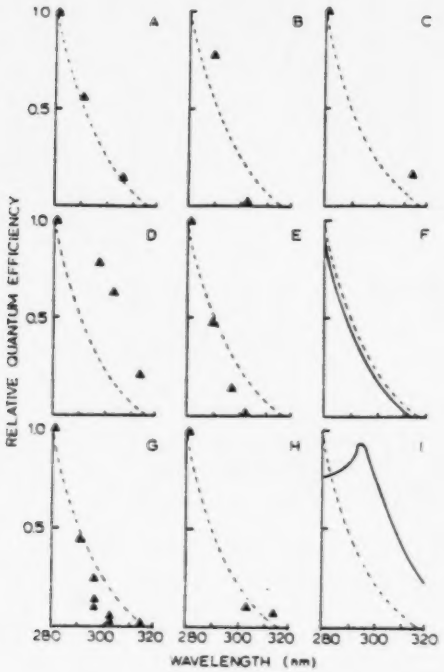

Figure 3. A generalized plant UV-B action spectrum relative to 280 nm (dashed line) as it corresponds to action spectra data for: A, mutation of liverwort spores, Sphaerocarpus donnellii (34), B, mutation in the fungus Trichophyton mentagrophytes (29); C, inhibition of photosynthesis in Chlorella pyrenoidosa (4); D, cessation of cytoplasmic streaming in epidermal cells of Allium cepa (26); E, frequency of "endosperm deficiencies" in maize due to chromosomal deletion or mutation (48); F, germidical action spectrum (38); G, epidermal cell damage in Oxyria digyna leaves (10); H, induction of chromosomal aberrations in Tradescantia paludosa pollen (32); I, base curvature of Avena coleoptiles (19). All of the action spectra have been expressed in terms of relative quantum efficiency which denotes either relative quantum effectiveness (spectra A, B, E, F, H and I) or relative quantum sensitivity (spectra C, D, and G). From Caldwell (11).

Significance for Plants of the UV-B Portion of Sunlight

The life of plants depends on different metabolic (cf. photosynthesis) or developmental (cf. photomorphogenesis) processes which are known to be regulated by certain spectral ranges in the visible radiation. Compared to total sunlight the UV-B (280 - 320 nm) portion is too small to be a factor in these basic photoreactions. Furthermore one must consider that UV-B radiation is strongly absorbed at the plants' surface and will not penetrate either to the inner cells of green leaves or of other plant organs which show reactions to light. So far there is no evidence for UV being essential for normal development of any higher plant species. Damaging effects which can definitely be explained by the influence of sunlight-UV have not been observed on plants in their natural habitat. The few harmless UV-effects known in a few specific plants could either be related to UV stress effects or to protection against possible UV damage and will be discussed in detail. It will be shown that plants have evolved highly effective protective mechanisms which allow them to tolerate permanent and in many cases even unreduced sunlight. Plants should therefore prove essentially less sensitive to increasing levels of sunlight UV than man and possibly some animals. It should be emphasized, however, that present knowledge on UV resistance of plants is very limited. As will be specified in this review we are unable to predict definitely the consequences of even a two- or threefold increase in shortwave sunlight UV which could result from man made disturbances of the stratospheric ozone layer.

Evaluation of UV-B Radiation Effects so far Observed in Plants

1. UV-effects from artificial light sources

Most of the photobiological work dealing with UV-actions has been carried out using UV radiation of wavelengths and intensities not representative of the natural solar UV radiation. Quarz-mercury lamps emitting monochromatic UV at 254 nm have been used for the induction of various deleterious effects. Typical stress phenomena observed include (10, 11, 12, 16, 17, 22, 37):

(1) strong accumulation of phenolic or flavonoid like pigments,

(2) loss of chlorophyll by indirect enzymatic destruction,

(3) occurrence of mutations,

(4) loss of growth hormones,

(5) inhibition of seed germination,

(6) disturbances in ion uptake and transport,

(7) reduced and irregular growth.

These and similar effects will also occur with unphysiologically high doses of radiation from the UV-B range, because as a rule the same cell compounds (proteins or nucleic acids) will be the primary receptors of UV. No conclusions concerning the limits of UV tolerance of plants can, however, be drawn from these experiments. UV radiation has been demonstrated to elicit detrimental effects resulting in reduced photosynthetic capacity (2, 5, 40). Most of the research on UV-effects on photosynthesis has been conducted with high intensity radiation from germicidal lamps at 254 nm. UV primarily affects not physiological processes such as photosynthesis per se but specific cellular constituents. Studies with

algae and isolated chloroplasts yielded fundamental information on mechanisms of UV induced injury did not, however, reveal what will happen to intact plants in their natural environment, as plants are able to avoid UV injury to internal parts by physical or chemical shielding. Considerable additional research is needed in order to better define the effects of UV on photosynthesis and the potential changes in agricultural productivity.

2. UV-effects from natural solar radiation

There is so far no evidence that solar UV is a limiting factor for any plant species in its natural environment. For a long time the stout habit and intense pigmentation of alpine plants were believed to be the result of intense UV irradiation; however, other environmental factors of this extreme habitat (e.g. low temperatures, high total solar irradiance) and also genetic reasons have now been found to explain these phenomena (10, 11). Solar UV-B radiation is known to produce specific effects on the synthesis of phenolic and flavonoid pigments like anthocyanin. This UV-induced pigment formation will be discussed as a protective mechanism. The UV part of sunlight is thought to cause reduced or, in some cases, abnormal growth of several wild and cultivated plants, under extreme growth conditions. UV is in particular active in interaction with additional stress factors like low temperatures, distinct UV effects being observed in high intermountain arid regions (23, 37, 45). These experimental results cannot be interpreted in terms of potential effects of certain UV levels, because quantitative interrelationships between UV loads and effects are unknown. Furthermore, the experimental conditions (deletion experiments) were of questionable validity.

UV-Effects to be Expected with Useful Plants in Consequence of Reduced Levels of Stratospheric Ozone

1. Experimental limitations

Experiments to answer the question of whether an increase in UV-B radiation flux can pose a problem to plant production are difficult to perform for the following main reasons.

(1) Large scale supplementation experiments (selectively enhancing UV-B loads) have so far not been carried out in the field because of technical difficulties and financial limitations (energy requirements).

(2) Deletion experiments in the field have been performed but are of questionable validity for evaluating UV- tolerance. Concomitant reduction of radiation from the visible range will result in side effects on photosynthesis, morphogenesis or photoreactivation (UV-protection).

(3) Most investigations of the effectiveness of UV have been carried out with single plants or plant organs under laboratory conditions. In order to answer the posed question, however, climate has to be controlled simulating natural growth conditions. Furthermore, this type of experiment only describes the UV action on the most

exposed parts of a vegetation system. Plants as a rule grow in communities (wild plants in ecological niches) partially sheltered from continuous direct beam solar radiation and in part from skylight as well. Plant species adapted to low intensity light, the UV part of which had been filtered out by shading leaves of other species, might be more susceptible to changes in UV radiation than plants thriving in high radiation regimes.

(4) If irradiations are carried out using solely UV in the absence of radiation of longer wavelength, plants would be deprived of photoreactivation and other photoprotective mechanisms. Therefore, damage might become apparent which would not have otherwise. On the other hand supplemental irradiations with light sources emitting besides UV large amounts of longer wavelength radiation might enhance photoreactivation to an extent not to be achieved under natural sunlight conditions. Irradiation techniques are badly in need of improvement (46).

2. Potentially UV-sensitive target areas of plants in different developmental states

In order to estimate potential UV damage on plants, UV sensitivity throughout ontogenesis has to be taken into account. This has not been considered in former investigations. During seed germination, the root until it has penetrated the ground, should be as UV-sensitive as other meristems or reproductive tissues. In many plants vegetative buds or floral primordia are highly exposed to high radiation loads. Pollen typically not distributed by wind may be susceptible. Special interest should be cast upon potential UV-effects on stomatal movement. Since the stomata of many plants including agricultural crops are also located on the upper leaf surfaces, the guard cells surrounding the stomata being the only photosynthetically active cells directly exposed to UV. The guard cells would be the most vulnerable of all chlorophyll containing cells. The light reactions of photosynthesis in these cells may be required to initiate stomatal opening. Even if UV does not directly affect photosynthesis, the overall efficiency of photosynthesis could be reduced as a result of CO_2 uptake limited by UV promoted stomatal closing.

In order to approach the problem of whether plant productivity will suffer from increased UV loads, susceptible targets have to be identified and analysed as to how far they would intercept radiation in the vegetative system.

3. Differential UV-B Sensitivity of Higher Plant Species

Another complicating factor in the assessment of the potential impact of reduced stratospheric ozone is the apparent differential sensitivity of higher plants to UV-B radiation.

Following the suggestions during the 1972-73 period that high altitude aircraft exhaust emissions might catalyze a partial destruction of the stratospheric ozone layer, the US Department of Transportation initiated the Climatic Impact Assessment Program. Although the program largely revolved around atmospheric chemistry and dynamics, a later phase involved biological studies to investigate the potential consequences of partial atmospheric ozone reduction.

The duration of the actual experimentation was rather brief--on the order of 18 months. Although necessarily of very limited scope, these preliminary studies provided some valuable information. It was demonstrated that UV-B radiation can elicit a number of detrimental plant responses such as reduced photosynthesis and plant growth, enhanced stomatic mutation rates, decreased pollen germination and some plant growth pattern abnormalities. Most of these effects were the result of rather intense UV-B irradiation corresponding to a much more severe ozone reduction than is presently contemplated. It would be very imprudent to attempt to extrapolate from these results to a consideration of the potential consequences of a moderate reduction of the ozone layer.

These studies also indicated that there is a substantial variation in the basic sensitivity of different higher plant species to UV-B radiation. Earlier studies by Cline and Salisbury (16) which employed very intense 254-nm radiation, also indicated substantial differences in species sensitivity to the radiation.

From the various experiments it is difficult to generalize about the basis of the differential species sensitivity to UV-B radiation. Although many of the sensitive species tended to be broadleaf species such as some of the leguminous crops like pea and bean, there is no general categorization that could be applied. Many graminoids were often less sensitive. However, several important graminoides of agricultural interest such as maize and rice displayed sensitivity in some of these experiments. The basic reasons for the differences in sensitivity between species are not at all clear. There were no striking correlations between sensitivity and parameters such as taxonomic affinity, growth form, or other overt plant characteristics. The differential sensitivity of species must, however, relate to their differences in capacity for coping with UV-B radiation.

The degree to which variations in optical properties of plants, such as leaf epidermal UV-B transmittance, and the efficacy of repair systems contribute to the apparent differential sensitivity of higher plants has not yet been elucidated. Nor have extensive studies been undertaken to evaluate the acclimation potential of individual plants to accommodate increased intensities of UV-B irradiance. This acclimation might be elicited by prior exposure to UV-B radiation or perhaps other environmental factors which might lead to a heightened tolerance of UV-B radiation.

Because of the tremendous diversity of plant life--particularly in non-agricultural ecosystems, some predictors of UV-B radiation sensitivity must be developed. It is inconceivable that even in an ambitious screening program that but a very small sample of the Earth's flora could be empirically tested for UV-B sensitivity. An assessment of the impacts of atmospheric ozone reduction on plant life should obviously be centered around those species which would be most sensitive to change in UV-B radiation. Thus, elucidation of the basis of differential sensitivities of species should be a very high priority

Although the recent preliminary experiments undertaken during the Dept. of Transportation program did not include any forest species, a limited number of coniferous species investigated in the study of Cline and Salisbury (16)

indicated many of these trees to be highly resistant to short term exposures to the very actinic 254-nm radiation. However, this should not be taken as an indication that forest productivity would not be affected in the event of stratospheric ozone decrease. Chronic exposure to even moderately increased UV-B radiation may be of consequence for coniferous species. The fact that most conifer species do maintain photosynthetically active needles for long periods of time would provide the opportunity for the accumulation of a substantial total UV radiation dose as was discussed in the earlier section.

4. Interactions of UV with other stress factors

UV radiation has to be regarded as one of several stress factors acting on plants in the environment. If a plant has to cope with another factor such as temperature stress or infection, an additional UV load might result in a detrimental response, while the same UV load was tolerated by the plant under optimal growth conditions.

In this context one positive prospect of an increased UV irradiation should be mentioned. It could be that some plant pathogens are damaged by UV to a greater extent than hosts themselves, or UV might induce alterations within the host (e.g. formation of antibiotic substances or morphological changes decreasing the susceptibility to pathogens. There are some minor experimental hints supporting even such a conception of (some) potentially beneficial consequences of an increase in solar UV radiation (3, 9, 31, 39, 53). Susceptibility of bean plants to virus (5) was found to be reduced and tobacco mosaic virus-RNA to be inactivated by UV (42/43). In any case interactions of this sort must be considered as possible complications for the interpretation of UV effects.

5. Experimental evidence for potential UV effects

In a series of recent laboratory studies, sponsored by the U.S. Department of Transportation, supplemental UV-B irradiations were used to simulate the effect of a 50% reduction of ozone (14, 15). From these investigations it can be concluded that, in response to the increased UV load, some agricultural plants (in certain developmental states) will be reduced in growth and in their capacity to photosynthesis. Seedlings were found to be more sensitive to UV than are mature plants. Great differences in UV-tolerance were observed among different species. The experiments, however, did not conclusively enough predict far-reaching consequences to increased levels of UV radiation on plant production. Nevertheless, these results support the view that an increased UV flux could pose a problem to agriculture.

It must be taken into consideration that unreduced plant productivity will require UV resistance not only of the mature plants. In many cases high germination percentage and vigorous seedling growth are essential for economical plant production. These young developmental stages might also suffer from UV stress. The influence of UV-B radiation from FS40 fluorescent sun lamps on germination and seedling development has recently been studied by Krizek (33). The UV effect was analysed on tomato, radish, cucumber, lettuce and bean and on field crops, such as wheat, cotton, soybean and millet. Germination was found to be not significantly influenced by UV. Abnormal seedling growth, however, was observed in response to continuous exposure to UV alone with all species but wheat. Seedlings were not grown under field conditions. Photo-reactivation or

photoprotection mechanisms could not become effective during UV treatments. UV-loads applied to the plants were much greater than those projected for a 50% decrease in stratospheric ozone. From these results one can only conclude that wheat seedlings will be extremely UV resistant and that seed germination of all tested species will not be effected by increased UV irradiation.

Cotton seedlings turned out to be very sensitive to UV stress (2). Laboratory studies of early seedling growth and of translocation of radiozinc from cotyledons showed that slight damage of the seedlings might occur under projected decreases in the ozone layer. These results also must be reproduced under field conditions using better simulated UV-B solar irradiation.

Two effects which are of particular ecological import are reductions in photosynthetic capacity and curtailment of leaf once expansion, both of which would contribute to an impaired carbon economy of the plant. Studies recently completed by W.B. Sisson (M.M. Caldwell, personal communication) with Rumex patientia exposed to various levels of polychromatic UV-B irradiance corresponding to solar UV-B irradiance at various concentrations of atmospheric ozone, provide some indication of the pattern of response to UV irradiance. For impairment of photosynthesis, response to $UV\text{-}B_{BE}$ was quite nonlinear and there did not appear to be a particular threshold of $UV\text{-}B_{BE}$ to which the plant must be exposed before photosynthetic damage ensured. Instead, reduction of photosynthetic capacity appeared to be only a function of the total accumulated exposure to $UV\text{-}B_{BE}$ and even UV-B irradiance corresponding to that under present-day ozone conditions resulted in some impairment of photosynthesis relative to control plants exposed to no UV-B radiation. Reciprocity in the response to $UV\text{-}B_{BE}$ applied over a considerable period of time (5 to 45 days) for individual leaves exposed to 3 levels of $UV\text{-}B_{BE}$ irradiance. Thus, damage to the photosynthetic system appears to be accumulative over a considerable portion of the ontogeny of individual leaves and is apparently only a function of the total $UV\text{-}B_{BE}$ to which the leaf is exposed. In terms of leaf enlargement, reciprocity did not apply over long periods of time. Instead, $UV\text{-}B_{BE}$ was most effective in curtailment of leaf expansion during only a period of two or three days during early developmental stages. The response was, however, a function of the level of $UV\text{-}B_{BE}$ irradiance during this short period of time. The reduction of leaf expansion rates appears to be due to effects of UV radiation apart from the simple limitation of photosynthate supply (47).

This study suggests solar UV-B irradiance, even under present-day conditions, may be a significant ecological factor for Rumex patientia. This species occurs in open habitats exposed to full insolation and there is a minimal degree of self-shading among leaves of the same plant. Individual leaves of this species are active for periods of time sufficient to accumulate appreciable exposure to solar UV-B radiation. The degree to which other higher plant species would correspond to this pattern of reduction in growth and photocynthesis as a function of UV-B irradiation is difficult to predict. Rumex patientia was selected in this study because it is both sensitive to UV-B radiation and exposed to full sunlight in nature. Many other higher plant species are, however, much less sensitive to UV-B radiation (8). Nevertheless, if the accumulative mode of damage to the photosynthetic apparatus is generally applicable to higher plants, even moderately UV-B resistant species may be affected by UV-B radiation in the event of ozone reduction if such species possess long-lived leaves which are exposed to full sunlight.

The effects of UV-B irradiance on photosynthetic capacity have been shown to be associated with the nonstomatal component of photosynthesis (47). That is, reduction of photosynthesis was not due to a simple increase in the diffusion resistance to CO_2 entering the leaf through the stomates. Instead, the damage appeared to be associated with the photosynthetic apparatus itself and related studies have shown that electron transport associated with photosystem II may be most affected. Since stomatal diffusion resistance did not change, the capacity for transpirational water loss would remain the same; therefore, the water use efficiency of photosynthesis (photosynthesis/transpiration ratio) would also become less favorable for a sensitive plant such as Rumex patientia exposed to UV-B radiation.

As there is no more relevant experimental data available, the following points of view need to be carefully considered for an evaluation of the consequences of an increasing level of UV radiation on utilized plants:

(i) Eliminating of one seemingly insignificant member of an agricultural or natural ecosystem might result in serious alterations in such balanced communities. For timber production natural systems are utilized which are not completely controlled by man and therefore might be indirectly influenced by UV in an unexpected way. Long-term development of a highly UV resistant tree might be limited by UV damage of some inconspicuous but essential organisms of the ecosystem.

(ii) If it turns out that certain effects of UV damage accumulate over a long time, as has been supposed by Caldwell (Book of Abstracts VII. International Congress on Photobiology, 58, Rome 1976) for the repression of net photosynthesis, even a slight increase in UV will become serious for plant productivity or maybe for survival by changing the competitive balance between species.

(iii) As a rule, cultivated plants are grown under conditions far from those of their natural habitat. That means plants will often not be adapted to UV loads to be tolerated in the field. For example, wind conditions may expose certain sensitive phyto-elements to solar UV radiation that ordinarily would remain sheltered under calm condition in another region. Distances in crop stands might be of importance for UV-tolerance.

(iv) It has to be considered that cultivated plants might have lost UV protective mechanisms by selection.

(v) There are some indications that UV might be much more damaging when plants are under competitive stress.

(vi) Productivity of certain useful plants depends on effective pollination by insects. Many insects are known to utilize UV for orientation. In case of altered UV intensities orientation might be disturbed and, therefore, the effectiveness of insect pollinators and maybe also of predatory insects be reduced.

(vii) It should be pointed out that knowledge about UV effects on aquatic (especially of marine) plants is of greatest importance, because primary production of the ocean depends on photosynthetic activity of these organisms. Clean water is not effective in absorbing UV-B radiation. Under laboratory conditions some single celled algae proved to be extremely sensitive to UV damage (14, 15, 28). There is no information at all about potential UV-effects upon planktonic organisms living in UV-transparent natural environments.

(vii) Although the relationship between ozone reduction and UV-B_{BE} has been calculated to show an approximate 2% increase in UV-B_{BE} per 1% decrease in ozone thickness, the physiological responses of plants reflecting the net unrepaired radiation damage is not necessarily a linear function of UV-B_{BE}. Thus, the question of the basic dose-response relationships must be addressed. Several related questions are also pertinent: Is there a threshold level of UV-B_{BE} to which plants must be exposed before physiological manifestations of unrepaired damage appear? Do plants respond to the total accumulated exposure of UV-B_{BE} or are the physiological manifestations better correlated with the level of UV-B_{BE} irradiance during rather brief periods of time such as during critical developmental stages.

Experimental data thus far available are not strong enough to predict severe damage to plants in response to increased solar UV irradiance. Even if plants will survive, however, there is good evidence that certain useful plants under unfavourable growth conditions will be influenced by UV in such a way as to result in reduced productivity.

Protective Mechanisms Against UV Damage in Plants

Plants vary widely in the extent of their response to UV radiation, depending on morphological, biochemical or physiological variables. Plants have evolved adaptive mechanisms for utilizing certain beneficial photoreactions at the same time protecting themselves against others. UV damages biological systems primarily through destruction of specific cellular constituents rather than alteration of broad physiological processes. It must be considered that the UV portion ($\lambda < 320$ nm) most influenced by changes in ozone concentration is also that most effectively absorbed by nucleic acids and proteins. Plants have developed three principle protective mechanisms to withstand UV damage:

(i) Plant organs or cell organelles are able to avoid high intensity light by orientation and UV sensitive tissues (meristematic and generative cells) are located several cell layers below the screening plant surface. Susceptible tissues like young vegetative buds, only covered by embryonic leaves, may be protected if growth takes place at night or in periods of light when the UV portion is low. Basic to this concept of avoidance would be plant processes altered in a positive manner by UV itself. Plants can respond to UV, selectively inducing physiological processes that might be linked to survival. Base curvature of Avena coleoptiles (19) and root elongation of several Umbelliferae seedlings (49, 50, 52) were found to be specifically

mediated by UV with a maximum response at about 295 nm. This type of UV effects have not yet been analysed in other plants.

(ii) Plants are able to shield themselves by coverings and pigments, mechanisms which at the same time often serve other purposes such as protection from infections or (from) oven transpiration. UV is absorbed and reflected by extracellular compounds such as cuticular substances and cell wall materials. Optical properties of such extracellular material vary considerably within single plant species or even within different parts of one plant, and will only in exceptional cases be a main factor in UV resistance (1, 11, 24). The thickness of an epidermis appears to influence the amount of UV radiation that penetrates cells lying below, but the biochemical potential of the epidermal cell will have a greater influence on the transmittance of UV. Transmittance through the epidermis of most higher plant leaves is on the order of 80 or 90% in the visible part of the spectrum and typically decreases to less than 10% in the UV-B portion of the spectrum (36, 10). Although the epidermis itself must be considered a physiological target of some importance, this selective absorbance of UV-B radiation by the epidermis undoubtedly reduces the impact of UV-B radiation on mesophyll tissues. Epidermises, when exposed to radiation in some cases quickly become impervious for UV due to the formation of anthocyanins or other flavonoid or phenolic compounds (10, 11). There are a few cases where flavonoid synthesis can be induced by UV itself (10, 11). A very sensitive UV effect on flavonoid formation was observed in parsley seedlings (49 - 52) with a maximum quantum efficiency at wavelengths near 300 nm. A linear relationship was demonstrated between UV dose and the amount of pigments. General distribution in the plant kingdom of highly effective defense mechanisms like this needs to be examined.

(iii) Reactions which reconstituate UV damaged nucleic acid molecules (esp. DNA) to the original state have been termed "repair mechanisms". Such processes have been shown in a wide variety of species and can be presumed to operate in all organisms (11, 18, 25, 28, 31). There are several different mechanisms of "dark repair" (30) (not molecularly understood in higher organisms) that might be of importance in reversing UV damage. "Photoreactivation" is of special interest with aspect to potential UV effects on plants, and must be considered as an interfering factor in all irradiation experiments. Photoreactivation is the reversal of UV damage to DNA the basic genetic constituent of cells and is brought about by radiation of longer wavelengths (blue-violet spectral range) of sufficient intensity. This energy is needed for the activation of the specific enzyme responsible for the repair process.

Photoreactivation has been demonstrated in a variety of higher plants for several physiological manifestations of UV irradiation at 254 nm (11, 18). A few studies also have demonstrated that some UV-B induced damage can be photoreactivated (10). It is quite likely that these molecular repair systems such as photoreactivation are of survival value to higher plants under present-day ozone conditions rather than being simply a vestigial element lingering

from earlier stages of the evolution of plant life during that time when the earth's ozone layer was only just forming.

The importance of photoreactivation for plants growing under a normal solar irradiation regime was implied in earlier experiments where leaves of several alpine plant species were exposed to 297- and 300-nm radiation with intensities controlled to closely simulate UV-BBE on a summer day at alpine elevations (10). During and following this irradiation, the leaves were not exposed to any other wavelengths. Some of these leaves did exhibit severe lesions indicating UV-Binduced damage which had never been observed under field conditions. The absence of such lesions in nature might suggest the importance of photoreactivation of UV-B-induced damage as an effective protective mechanism. Photoreactivability of these UV-B-induced lesions was also shown on these studies.

It should be pointed out that photoprotective mechanisms (41) and photoreactivation respond to visible light. Since UV and visible are under present conditions highly correlated, the avoidance responses to one serve as mechanisms for avoiding the other. The increase in UV, however, which would result from a decrease in ozone would be disproportionately large in relation to total solar radiation and therefore protective reactions would not be adapted to the increased UV level.

Ecological Implications of Ozone Reduction

Although there is little doubt as to the destructive potential of solar UV-B radiation for at least sensitive higher plant species, the probable ecological impact of increased UV-B radiation resulting from decreased mean atmospheric ozone concentrations is difficult to assess. For agricultural or forest species which are sensitive to UV-B radiation, it is very conceivable that even the increase of UV-B radiation that would result from moderate ozone reduction may have effects on productivity. Since both photosynthesis and leaf expansion are critical to plant productivity and are processes readily affected by UV-B radiation, impacts on plant production and yield may be expected if the species in question are sensitive to UV-B radiation.

Because higher plant species do appear to be differentially sensitive to UV-B radiation another consequence of changes in UV-B radiation may be a shift in the competitive balance among species in nature.

With ozone reduction, even small depressions of photosynthesis, growth, or water use efficiency of photosynthesis caused by exposure of sensitive species to increased UV-B radiation may under some circumstances shift the competitive balance in favour of more UV-B-resistant species. Recent experiments in M.M. Caldwell's laboratory by F.M. Fox (personal communication) suggest that the competitive balance between species can be changed with even modest supplements of UV-B radiation.

Although it has never been documented or perhaps even much contemplated, some shifts in competitive balance between higher plant species may be taking place during the course of natural fluctuations in atmospheric ozone. Natural fluctuations of the ozone column occur over periods of days, months, and years. During the course of frontal storm system movements in mid-latitudes, the

atmospheric ozone column over a given locality can change by a magnitude of 20 to 40% in a few days time (20). However, such short-term changes are probably of little influence since in most cases plants would be responding to the average UV-B flux over a longer period of time. (As was discussed earlier plants appear to be subject to an accumulative UV dose.) Seasonal variations of 20 to 40% also take place in middle latitudes, the high concentrations occurring in the spring and low concentrations in the fall (20). However, because these changes are phased with the seasonal change of prevailing solar angles from the zenith, they merely modify the present variations in monthly average UV-B radiation at different times of the year. Although seasonal changes of ozone probably exert little change on the competitive balance of species, the seasonal timing of major periods of photosynthetic activity and growth of UV-B sensitive plant species may have adjusted in the course of evolution to avoid, to a certain extent at least, periods of particularly high UV-B flux during the year.

In terms of changes in competitive balance among plant species, it is the variation of ozone over the course of several years which would be most influential. Long-term records of atmospheric ozone concentrations are unfortunately very limited. At only a couple of geographical locations do records covering even the past four decades exist. Nevertheless, such records bear some witness to changes in mean annual concentration for about 10% which appear to follow an approximate 10- to 12-year cycle (20, 13). These changes would result in roughly a 20% change in $UV\text{-}B_{BE}$ over periods of half a dozen years which might result in some shifts in competitive balance of species. Though evidence for changes over longer periods of time do not exist, they might be expected. For example, if the periods of low ozone during the 10- to 12- year variation are indeed linked to periods of low sunspot activity, with appropriate lags, as has been suggested by Christie (13), periods when there was an extended lull in sunspot activity such as has been suggested to have occurred during the latter part of the 17th century (21) may have resulted in an extended period of low ozone concentrations. Unfortunately, a retrospective surmise as to the biological consequences of such extended periods of low ozone concentration, or even during the course of the 10- to 12-year fluctuations, has not been attempted and would undoubtedly be difficult, if not impossible.

The natural fluctuations of ozone concentration, particularly over the longer term, do, however, suggest that higher plants, and ecosystems in general, must display a certain resiliency and ability to accommodate some change in UV-B flux. Although the basic character of an ecosystem might show little change during the course of long-term ozone fluctuations, it would not be unreasonable to expect some shifts in species prevalence during these periods.

The magnitude of change over the 10 to 12-year cycle, i.e. 10%, is at least equal to the ozone reduction anticipated from several man-induced depletions of atmospheric ozone. Nevertheless, the anthropogenic reduction of mean atmospheric ozone would be superimposed on natural fluctuations. Therefore, periods of low ozone concentrations in the course of natural variations, if compounded by a man-induced reduction in mean ozone concentration, could result in exposure of ecosystems to UV-B flux not yet experienced in particular regions.

Mean ozone concentrations also vary considerably with geographical location. This is primarily a function of latitude, with lower concentrations toward the equator. Although this natural ozone gradient has been useful in deducing possible trends in human skin cancer, analogous inferences concerning

higher plant response to UV-B radiation are not so feasible. Plant response to this UV-B gradient is confounded by the influence of other environmental factors such as temperature and moisture supply on plant growth and success.

Since the ozone depletion question as it relates to ecological consequences is restricted to a very narrow waveband of the solar UV spectrum (see Figure 1), it is perhaps not surprising that a background of scientific information upon which to base an assessment does not exist. Due to the lack of particular scientific attention to this narrow waveband, compounded with the problems of generating UV-B flux of appropriate intensities and wavelength composition, few studies dealing with UV-B had been undertaken until the questions of man-induced ozone depletion came to the fore. A concerted effort to place some perspective on the ecological consequences of ozone depletion on the order of 15% or less is, however, urgent in the face of current trends in stratospheric flight and the release into the troposphere of agents which can be calculated to have potential ultimate consequences for the global stratospheric ozone layer.

Summary

The biological impacts of an increase in solar UV radiation as would result from ozone destruction are evaluated preferably in consideration of potential effects on economically important plants.

Although there are natural fluctuations in the ozone layer any man-induced reduction of the ozone layer would be superimposed on the natural fluctuations and would be justifiable cause for concern.

Proteins and nucleic acids are the compounds in living beings most susceptible to UV radiation from the spectral range below 320 nm (UV-B). Where these compounds are the UV receptors, biological effectiveness of UV will increase exponentially with decreasing wavelengths. The effectiveness of atmospheric ozone in filtering out UV is highest at lowest wavelengths of solar radiation. These are the two reasons why even minor increases in the range of shortest wavelengths of sunlight in response to ozone destruction might result in distinct - as a rule damaging - biological effects.

For each 1% reduction in the atmospheric ozone column there would be a predictable increase of approximately 2% in solar UV radiation when weighted for biological effectiveness.

Plants are able to protect themselves very effectively from UV radiation

by movement of organs (e.g. leaves) or cell organelles to avoid intense irradiation,

by surface coverings (cuticula, cell walls, layers of dead cells),

or pigments accumulated in the outer cell layers (epidermis).

There are a few examples where pigment formation can be adapted to UV levels. In many cases, however, plants respond to total radiation and not UV selectively for protective reactions.

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Finally all organisms are considered to possess a variety of molecular systems in order to repair UV mediated disruptions of nucleic acids. Photoreactivation should be very important for plants in preventing UV damage to DNA.

It has been found that plant species differ significantly in sensitivity. UV levels which can no longer be compensated by protective mechanisms are unknown for plants in natural or agricultural habitats.

Functioning of an ecosystem depends on the well balanced interrelationships between different species and UV damage to one organism might finally result in dramatic effects upon another one which is UV resistant. In this indirect way timber production might be negatively influenced.

Since both photosynthesis and leaf expansion are critical to plant productivity and are processes readily affected by UV-B radiation, impacts on plant productivity and yield may be expected if the species in question are sensitive to UV-B radiation.

So far there is no convincing evidence that any plant species would not withstand an increase in biologically effective UV corresponding to a 50 percent decrease in stratospheric ozone. Minor UV effects (e.g. on growth or photosynthesis) potentiated by additional stress factors might result in long-term consequences for the survival of certain plants and very likely for productivity of cultivated plants.

Considerably more research is needed before the consequences of an increased UV-B radiation on plants in natural or agricultural ecosystems can be calculated.